# THE FORMATION OF NEW COLONIES OF THE ROTIFER, MEGALOTROCHA ALBO-FLAVICANS, EHR.

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Colony formation is not common among the Rotifera. But in several species, belonging especially to the family Melicertidæ, the individuals do become aggregated into colonies. These animals do not reproduce by budding, as do so many colonial forms, nor in most cases does the colony contain the progeny of its members. Instead, the young are hatched as free swimming individuals which later become segregated into a separate fixed colony.

During the past winter, while a graduate student at the University of Pennsylvania, the writer made some observations on the formation of new colonies of *Megalotrocha alboflavicans*. Colonies of this large rotifer were found in abundance in the fresh-water tanks of the vivarium, whither they had been transferred some years before from the small pond in the botanical gardens. These colonies are ordinarily formed on the roots and stems of various water plants, but in the vivarium they were found only on the stems of *Myriophyllum*. The colonies are nearly spherical in shape and when adult may measure as much as 4 mm. in diameter. They are thus easily recognizable to the unaided eye, appearing as white spots on the dark or green stems. The colonies used were kept in glass jars in the laboratory and for observation a piece of the stem containing a colony was removed, placed in a small dish and observed with a Braus-Drüner binocular.

The work was undertaken at the suggestion of Professor E. G. Conklin, and it is a great pleasure to acknowledge my indebtedness to both him and Professor H. S. Jennings for their many valuable suggestions and kindly criticisms.

The colonies of *Megalotrocha* are not surrounded by gelatinous masses or tubes as are certain other species of the Melicertidæ.

The animals are however attached to the stem by a kind of mucilaginous substance secreted by a gland in the foot. This substance forms a thin layer on the stem over the area of attachment of the colony. The adult colonies usually contained eggs or at least soon produced them after being brought into the laboratory. The eggs are attached to the mother by means of an adhesive gland situated a short distance posterior to the opening of the cloaca. Usually only one or two eggs are found attached to a single individual, but sometimes as many as four were observed.

The method of egg deposition is interesting. The egg rapidly increases in size in the region of the vitellarium, and then passes slowly down the oviduct to the cloaca. When the egg with its large germinal vesicle has reached this region the animal bends towards the dorsal side in such a manner that the adhesive gland touches the protruding egg. The animal frequently remains in this position for some time, often bending still farther so that the corona points towards the foot. In this way the end of the egg is firmly pressed against the adhesive surface of the gland. The animal now slowly and by repeated attempts straightens itself and at the same time the egg is pulled from the cloaca and remains attached to the mother, where it undergoes development. One egg has scarcely been deposited before another can be seen enlarging in the region of the vitellarium. Eggs begin to form in all the individuals of a colony at approximately the same time. But an interval of three or four hours may elapse from the time the first egg is laid until all the animals have deposited eggs. During this time the individuals which deposited the first eggs have often deposited a second. This overlapping of broods is important, as will be pointed out later, in keeping the size of the colonies more nearly constant.

The length of time required for the young rotifers to hatch varies somewhat, depending on the temperature and other conditions. Usually they hatch in three or four days after deposition. The young rotifer when fully formed can be readily seen through the transparent egg membranes. For some hours before hatching frequent contractions of the body and movements of the cilia and mastax may be seen. By means of these contractions the

young animal finally bursts the enveloping membrane and is able to swim about. The young rotifers possess an organization in most respects similar to the adult. But among the more important differences may be mentioned the following. The trochal disc is at this time no broader than the trunk, the whole animal tapering slightly towards the foot. At the foot there is a circlet of small cilia. On the anterior border of the trochal disc, near the dorsal side are two red eye spots which are lacking in the adult. The cement gland in the foot is proportionately larger in the young animal than in the adult.

The young rotifers are free swimming, but are always attached at the posterior end by a thread of adhesive material which they spin out much after the fashion of a spider. They swim about among the adult rotifers, sometimes venturing a short distance beyond the limits of the colony but always drawing back and continuing to move about among the old animals. During all this time they are attached to the old colony by the adhesive thread from the foot. By a continuation of this nervous crawling and swimming some of them finally get their webs so twisted together that they are brought into contact. Here they remain, apparently without secreting more of the adhesive thread. At first there are only two or three individuals thus approximated and these are near the center of the old colony. Soon other young rotifers get their webs entangled with that of the few aggregated ones and these are then added to the ball that is forming. Here as well as later, contact with the adhesive thread appears to act as a guiding stimulus to the young rotifers. As soon as a young animal comes in contact with the rather thick thread leading to the forming ball, it at once begins to move up or down this thread until it finally reaches the ball; this I have repeatedly seen. Usually the young animal does not at once attach itself to the ball, but continues to crawl about, often through the bunch of young rotifers. In this way it finally becomes attached to its comrades with its foot closely adhering to theirs. During all the time that the ball is forming, the individuals composing it act in a very nervous manner, constantly jerking, twisting, contracting and expanding in a most irregular way. By means of this continual twisting and squirming the forming ball succeeds

in stretching the thread holding it fast, so that later it comes to lie outside the limits of the old colony (Fig. 1). In the course of time this thread breaks and the young ball swims away.

From the time the first individuals are hatched until the ball breaks loose there is usually a lapse of three or four hours. Since all the eggs of one brood are not deposited at the same time the period of hatching often extends over several hours. The long time that it takes for the ball to form and break away gives opportunity for the later individuals to hatch and get into the new colony. Often there are a few young that do not get

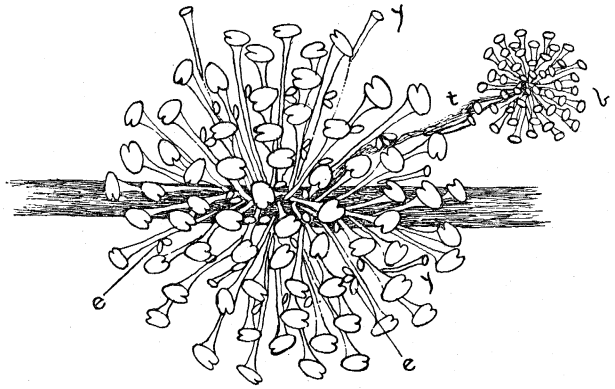


FIG. 1. Sketch to show formation of the swimming ball. *e*, eggs, attached to the adults; *y*, young animals before coming into the ball (*b*); *t*, mucilaginous thread holding the ball to the mother colony.

into the ball before it breaks away. These swim about for a time near the old colony and then may settle down on a near-by stem. Apparently these do not long survive the attacks of their enemies, for later I have seldom been able to find them, and I have never seen an isolated adult. By thus losing a few individuals in every generation the colonies would evidently continue to get smaller, for after the ball breaks away no new individuals are added to the colony. Such a decrease in numbers would undoubtedly take place were it not for the overlapping of the broods. One generation of eggs is laid so soon after the other that, in many cases, a large number of the second brood hatch in time to get into the forming ball. Occasionally, but not often,

two balls are formed at the same time, thus dividing the young colony.

The ball of young individuals is spherical in shape and is very regularly formed. Indeed, this is one of the very striking things about these interesting balls. The feet of the individuals are not attached together in an irregular mass, as one might suppose, but they are arranged so as to form a very regular sphere. It is difficult to ascertain just how the animals are held together in these balls, but it seems probable that they are glued by the adhesive substance from the foot gland. This is supported by the fact that when a young ball is killed and placed in alcohol it breaks up, as if the adhesive material had been dissolved. The animals when in this ball are always nervously jerking back and forth. The ball swims freely by means of the currents from the trochal discs. If, for any reason, more of the individuals turn their trochal discs in a certain direction, the whole colony will move in that direction. That the movement of the ball is due to the summation of currents is shown by mixing some india ink with the water. It is then seen that the ball always moves in the direction from whence the stronger current comes. The ball swims with a revolving motion but is nevertheless able to move with considerable precision in a certain direction. A most important characteristic of these young balls is the fact that they react positively to light. One always finds them on the side of the dish next to the window. If they are placed in a dish in the sunlight, the balls congregate on the side towards the sun. If this region is shaded they *at once* leave it and move towards a part more strongly lighted. A considerable number of experiments showed that this reaction is very marked and constant.

The time which the animals spend in this swimming ball before settling down to form a permanent colony varies considerably, depending primarily upon the illumination. So far as I have observed, the colonies usually hatch out during the morning hours, the young ball breaking away about noon or afterwards. In no case have I seen them, under natural conditions, form a colony until evening or after sundown. As long as the dish is lighted, even by diffused light, the young rotifers continue to swim back and forth along the lighted side of the dish, striving apparently

to get as near the source of light as possible. But if the ball is placed in artificial darkness they very soon begin to form a permanent colony.

The method of forming this permanent colony is interesting. When no longer influenced by the light the ball begins to move about the dish in an apparently aimless manner. If in this wandering it chances to come against some piece of water plant or other object many of the young rotifers turn their trochal discs towards this, thus checking the progress of the ball. This reaction is brought about by purely tactile stimuli. If a clean needle is placed in front of a swimming ball, the latter will stop and the young rotifers move their trochal discs along the needle. Whether they will settle down and establish a colony seems to depend chiefly on food conditions. If the stem possesses but little débris the ball may move along it for some distance, but in most cases finally swims away. If, however, the stem has more débris attached to it the young rotifers persist in their efforts to place their trochal discs on this, probably in order to get the food particles. In this way the ball is prevented from moving away. If the ball remains in one place for a time, one or two of the rotifers will be seen dragging themselves out of the ball and moving slowly along the stem. In this manner they move a short distance and then jerk back, then start out again, each time going a little farther. Soon others come out of the ball and begin moving about, until a large number are found moving up and down the stem (Fig. 2). In moving along the plant the animals extend their bodies with the long axis parallel to that of the stem. A few of the cilia of the trochal disc and a few of those in the posterior circle appear to touch the stem and in this manner the animals "crawl" along the plant, reminding one very much of a brood of young caterpillars. But it is probable that the water currents are here as at other times the most effective agents of locomotion. In these movements there is no revolution on the long axis. In advancing along the stem the animal usually shows great hesitation in going over portions which have not been traversed by some member of the colony. In the space over which several rotifers have travelled others move with little hesitation, but on coming to new territory they move forward a

short distance and then draw back, often repeating this several times. Thus each individual pushes some distance beyond the previous limit, but at last it usually turns around and moves back towards its fellows. This like certain observations previously mentioned seems to indicate that the adhesive thread which they always secrete as they move about, furnishes a guiding stimulus for the young rotifers. Sometimes an individual leaves the stem and swims a short distance from it, always attached by the thread.

By such movements the whole ball finally breaks up and the individuals are seen moving back and forth along the stem, some-

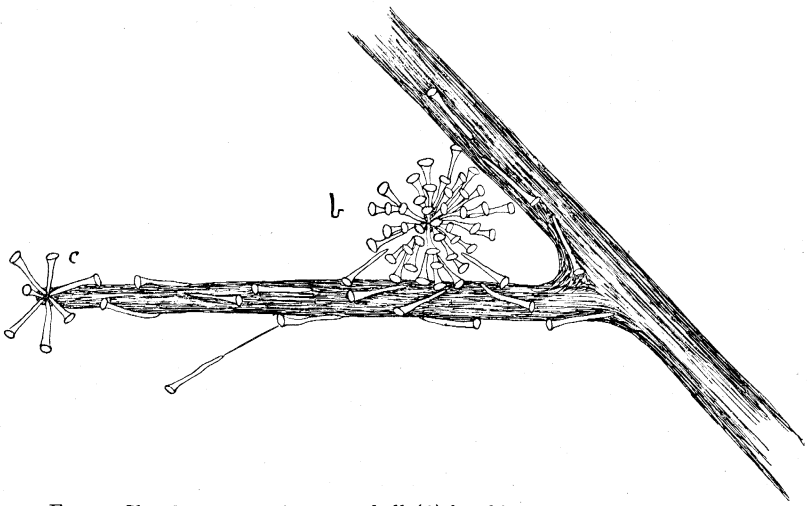


FIG. 2. Sketch showin the young ball (*b*) breaking up into free swimming individuals and the permanent colony forming at *c*.

times venturing quite a distance from the majority of the colony. But soon a few individuals settle down at some point and remain fastened by their posterior ends, with the body projecting at right angles from the stem (Fig. 2, *c*). Soon other individuals attach themselves in a similar manner with their posterior ends close to those already attached. This is the beginning of the formation of the permanent colony. In a comparatively short time all of the young animals have attached themselves in a closely aggregated group surrounding or nearly surrounding the stem. This permanent colony may be formed close to where the ball broke

up or at some distance from it. Sometimes it is formed at the end of a branch, sometimes at its base, or even on the main stalk; at other times in intermediate positions. If the swimming balls are allowed to remain in a dish containing no water plants soon after dark they begin to form a colony on the sides or bottom of the dish. Apparently when the stimulus from the light is removed the colony-forming instinct becomes dominant. When the young balls are placed in artificial darkness, colony-formation begins in from fifteen to thirty minutes and is usually completed within an hour or an hour and a half. Most of these colonies are found in well-lighted places. This doubtless arises from the fact that the swimming balls remain on the lighted side of the vessel and tend to form a permanent colony soon after this stimulus is removed. This is of advantage to the animals for they feed partly on diatoms and small protozoa which are more abundant in favorably lighted places.

Thus the young rotifers tend to remain attached in the swimming ball during their natatory life, but at the proper time they are able to sever this connection and to leave the ball one by one. Possibly the stimulus due to the contact of their posterior ends is sufficient to keep them together, until some stronger stimulus, such as food, overcomes the contact stimulus and induces them to separate. Hunger satisfied, they again respond to the stimulus of mutual contact and assemble anew, this time to form a permanent colony.

With the formation of this permanent colony changes take place both in the behavior and in the structure of the animals. Up to this time the young rotifers have behaved in a very nervous manner, constantly contracting and extending the body. But as soon as the animals settle down in the permanent colony they lose much of this irritability and remain with body and trochal disc expanded for long periods. Yet even in the adult colony one individual or another is frequently seen to suddenly fold the trochal disc and strongly contract the body, then at once begin to expand more slowly. Sometimes this contraction is evidently a reaction to some floating particle that has touched the trochal disc. More frequently there is no visible cause for the contraction. The animals in the permanent colony have another method

of reacting, not found or at least not so well marked, in the free swimming balls. When the colony is stimulated as by a slight jar to the dish or a disturbance in the water the whole colony contracts at once and if the stimulus is strong they may remain contracted for some time. This is the usual method of reacting to mechanical, chemical or electrical stimulation.

After the young animals have once formed a permanent colony they become incapable of repeating the colony formation. If some of the individuals of a permanent colony are removed from the stem they do not behave as they did previous to the formation of the colony. They swim about by means of the ciliary currents, but in an entirely aimless fashion. They neither attach themselves to the old colony nor form a separate colony. I have kept such removed individuals alive for several days but during this time they made no attempt to reform a colony.

There are likewise several structural changes which take place after the formation of the permanent colony. The animals soon show considerable increase in size, the trochal disc becomes broader and the notch on the ventral side of this makes its appearance. The small circlet of cilia at the foot of the animal disappears and the character of the cement secreted by the foot-gland changes. This cement is no longer dissolved by alcohol as it was in the young specimens. The gland is always much smaller in the adult than in the free swimming individual. But the most striking change and one which perhaps accounts for some of the changes in behavior, is the degeneration of the eye spots. As stated before, the rotifers when hatched possess two red eye spots; the reaction to light of the swimming ball is probably due to these structures. After the permanent colony has been formed for several hours one finds that the eye spots have disappeared from their previous position while two small red bodies are floating about in the body cavity. In most cases these bodies are inclosed in floating corpuscles which have considerable resemblance to leucocytes. Montgomery ('03) mentions the presence of certain non-cellular corpuscles floating in the body cavities of certain Flosculariidæ. He regards these as waste products. Since in *Megalotrocha* these bodies often enclose the degenerating eye spots and these latter are seen to

gradually waste away, it seems possible that they may function in the same manner as the leucocytes of many other animals. After the eye spots have disappeared from their original location the animals no longer react to light.

## General and Comparative.

The main features in the formation of new colonies of this rotifer are then as follows: When first hatched from the eggs the young are free swimming, but do not leave the colony singly. These individuals come together into a swimming ball which reacts positively to light. Later under certain conditions this breaks up into free individuals again. These then aggregate themselves into a permanent colony in which the animals spend the remainder of their lives. In this colony formation the mucus-like secretion of the foot-gland plays an essential part.

The details of colony formation in other rotifers has apparently not been described, but it seems probable from the known facts that a similar sequence of processes occurs in some other cases. In *Lacinularia socialis* according to Huxley ('53), Hudson and Gosse ('89) and others, the process appears to resemble that in *Megalotrocha*. The young animals come together into swarms or balls and swim freely. Later permanent colonies are found on water plants. In two species of *Megalotrocha* from China, *viz.*, *M. semibullata* and *M. spinosa* described by Thorpe ('89 and '93), the adult colonies are free swimming. In these cases the eye spots are present in the adults. The new colonies swarm out of the old free swimming ones. Occasionally these balls may be found suspended from aquatic plants by mucilaginous threads. In the genus *Conochilus* we find swimming colonies of a slightly different nature. Here the free swimming balls consist of several adults with many of their young. According to Hudson and Gosse many of the newly hatched rotifers make a place for themselves in the adult ball by squeezing between the older members, while others of the new brood form new balls and swim away. There are several other more or less rare species of Melicertidæ in which free swimming or fixed colonies have been described. The free swimming adult colonies are interesting as apparently marking a step in the formation of the

fixed colonies. While the occurrence of colonies or swarms is common in the animal kingdom, I have seen no accounts of colony formation in other groups that resembles the processes seen in these rotifers.

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## LITERATURE CITED.

**Huxley, T. H.**

'53 Lacinularia socialis; a contribution to the Anatomy and Physiology of the Rotifera. Trans. of the Micros. Soc. of London, N. S., Vol. I., pp. 1–19.

**Hudson and Gosse.**

'89 The Rotifera. Two volumes, London.

**Joliet, Lucien.**

'83 Monographie des Melicertes. Arch. de Zool. Exp. et Gen., 2e Series, Tome I., pp. 131–224.

**Montgomery, T. H.**

'03 On the Morphology of the Rotatorian Family, Floscullariadæ. Proc. Acad. Nat. Sci. of Philadelphia.

**Thorpe, V. Gunson.**

'89 Description of a New Species of Megalotrocha. Journ. Royal Micros. Soc., pp. 1–4.

'93 The Rotifera of China. Journ. Royal Micros. Soc., pp. 145–152.